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Nymphs of a new family Neazoniidae fam. n. (Hemiptera: Fulgoromorpha: Fulgoroidea) from the Lower Cretaceous Lebanese amber

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ABSTRACT

New species of extinct Fulgoroidea from the Lower Cretaceous Lebanese amber, *Neazonia tripleta* sp. n., *Neazonia immatura* sp. n., and *Neazonia imprinta* sp. n., are described as members of a new genus *Neazonia* gen. n. Descriptions are based on a IIIrd instar nymph, the exuvium of a Vth instar nymph and a cast in amber of a probable IIIrd instar nymph. The new extinct family Neazoniidae fam. n. is established for these fossils. Morphological characters and their importance in reconstructing evolutionary patterns of Fulgoroidea are discussed.

KEY WORDS: Hemiptera, Fulgoroidea, Neazoniidae, Lebanese amber, Lower Cretaceous, nymphs, morphology, coevolution, new taxa.

INTRODUCTION

The Fulgoroidea is a highly variable group of the Hemiptera and consists of two extinct (Fulgoridiidae and Lalacidae) and 21 currently recognised extant families. The recognised family groups include extant Achilidae+Achilixiidae, Caliscelidae, Cixiidae, Delphacidae, Derbidae, Dictyopharidae, Eurybrachidae+Gengidae, Flatidae+ Hypochthonellidae, Fulgoridae, Issidae+Acanaloniidae, Kinnaridae+Meenoplidae, Lophopidae, Nogodinidae, Ricaniidae, Tettigometridae, Tropiduchidae. The taxonomic status of some of these is not resolved. Achilixiidae used to be treated as representatives of a distinct family (Wilson 1989); they have since been included in Achilidae as subfamilies Achilixiinae and Bebaiotinae by Emeljanov (1991), or recently moved to Cixiidae, as proposed by Liang (2002). Kinnaridae appears to be a paraphyletic unit within the Meenoplidae (Bourgoin 1993). Gengidae could be united with Eurybrachidae, and Hypochthonellidae with Flatidae (O'Brien 2002). Issidae have recently been redefined, with Caliscelidae recognised as a distinct family (Emeljanov 1999). Acanaloniidae have been subsumed within Issidae (Fennah 1954; O'Brien 2002), but Emeljanov (1999) resurrected the family, incorporating the issid subfamilies Tonginae and Trienopinae within it, and placed Acanaloniidae as sister or daughter taxon of Nogodinidae. The monophyly of the Cixiidae has also been challenged (Holzinger *et al.* 2001). There is no agreement between different phylogenetic relationships within Fulgoromorpha (and Fulgoroidea) based on morphological evidence (Asche 1988; Emeljanov 1990; Yang & Chang 2000), molecular evidence (Bourgoin 1997) or combined morphological, palaeontological and molecular data (Bourgoin & Campbell 2002).

Studies on the nymphs of extant Fulgoroidea have advanced considerably in the last two decades (Emeljanov 2001). Fossil nymphs, in contrast, have been little studied (Szwedo *et al.* 2004). A fossil nymph suggested to be related to Fulgoroidea is *Knezouria unicus* Jell, 1993, reported from the Late Triassic, Carnian of Dinmore, Ipswich Basin, Queensland, Australia (Jell 1993). However, several critical characters are unclear and the placement of this taxon is inconclusive. The Lower Cretaceous fossils described below are representatives of the Fulgoroidea. There is no way of determining their morphogenetic development and they cannot be assigned to any known family, therefore a separate family and genus is erected for them.

TAXONOMY

Order Hemiptera Linnaeus, 1758
Suborder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Kirkaldy, 1907
Family **Neazoniidae** fam. n.

Type genus: *Neazonia* gen. n.

Diagnosis: In general habitus similar to some nymphs of Cixiidae and Achilidae, but distinctly flattened and more elongate. Differs from nymphs of any other Fulgoroidea in peculiar agglomeration of sensory pits on frons and abdominal tergites (arranged in rows in other Fulgoroidea) and pattern of sensory pits in groups of three or four.

Genus **Neazonia** gen. n.

Etymology: From classic Greek "*neâzon*", meaning "acting like a youth". Gender feminine.

Type species: *Neazonia tripleta* sp. n., by present designation.

Diagnosis: Body slender, somewhat elongately ovoid. Head with vertex about as long as wide; face elongate, with two submedian carinae, converging at fronto-clypeal suture. Rostrum elongate, extending beyond apex of pygofer. Two rosette-like groups of sensory pits on frons, not arranged in rows. Sensory pits on thorax and abdominal tergites not arranged in rows, but rosette-like. Prothoracic tibia quadrangular in cross section, with rows of short setae along margins. Mesothoracic tibia subquadrangular in cross section. Metathoracic tibia round in cross section with apical row of teeth, but lacking lateral spine; basitarsus distinctly elongate, with apical row of teeth. Second metathoracic tarsomere of last instar short, with row of apical spines bearing subapical setae. Pygofer with distinct median fissure ventrally.

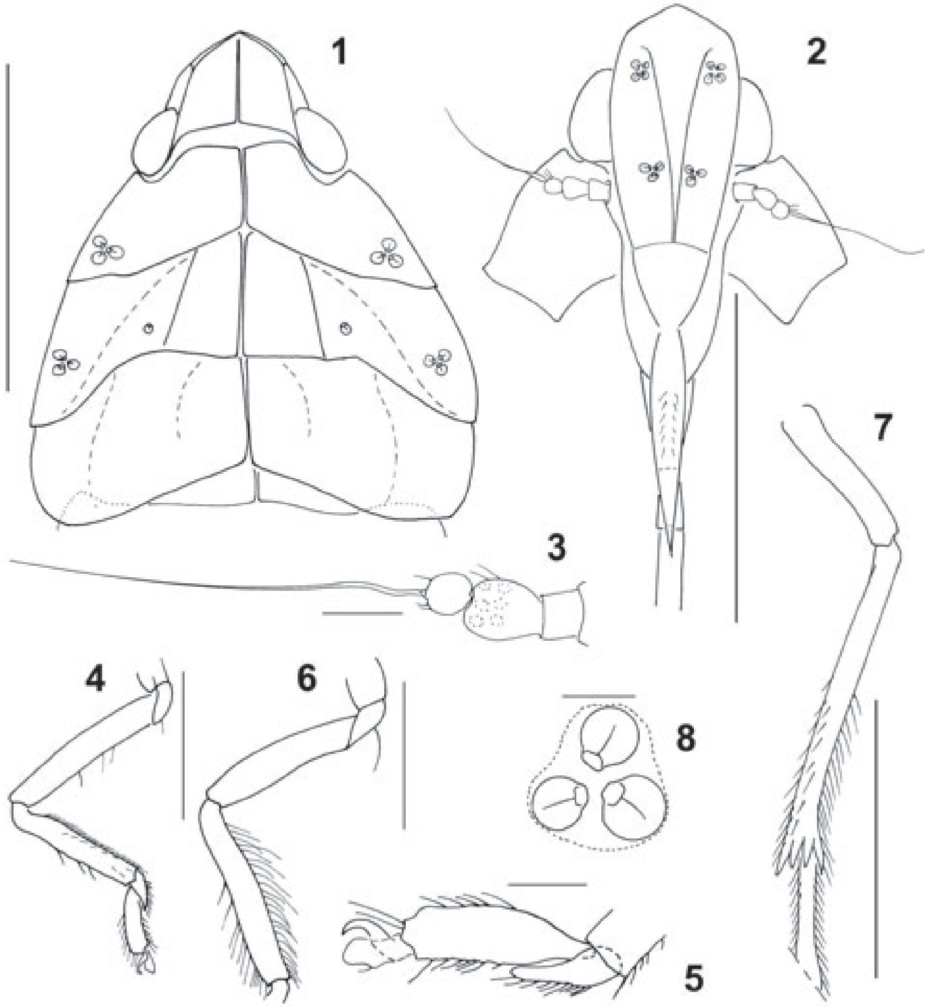
Species included: *N. tripleta* sp. n., *N. immatura* sp. n., *N. imprinta* sp. n.

Neazonia tripleta sp. n.

Figs 1–11, 24, 25

Etymology: Specific epithet refers to triplets of sensory pits on thoracic wing-pads and abdominal tergites.

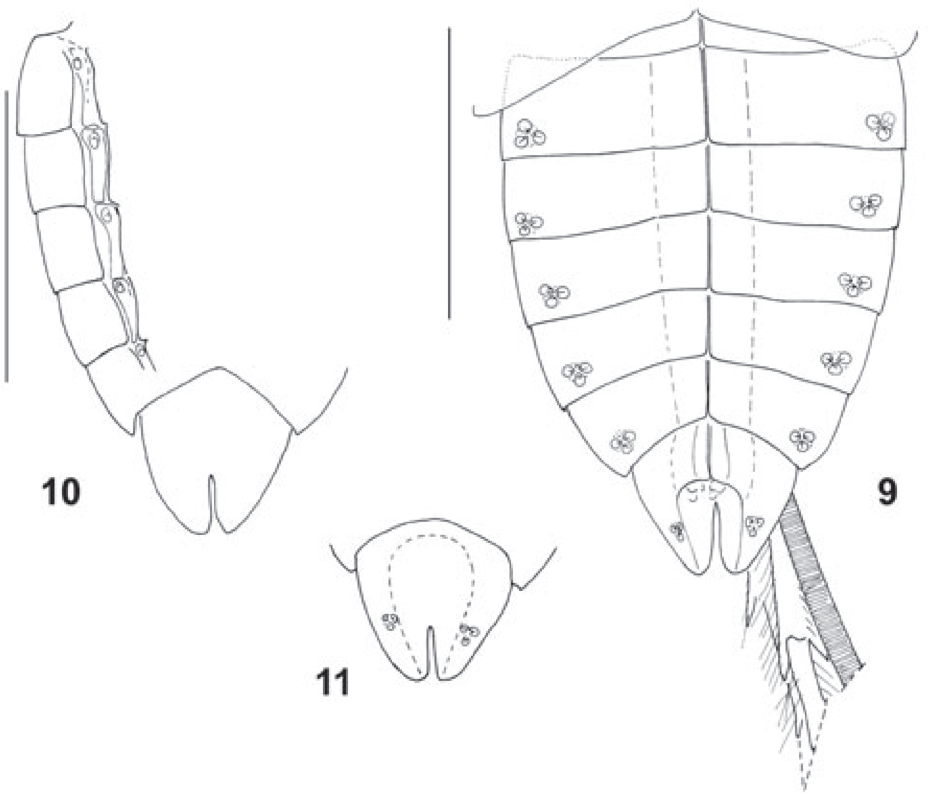
Diagnosis: More flattened dorso-ventrally than *N. imprinta*, not as elongate as *N. immatura*. Pronotum with group of three sensory pits at posterior angle (quadruplet and pentaplet near mid-line and another quadruplet at posterior angle present in *N. imprinta*). Anterior margin of pronotum distinctly incised (not incised in *N. imprinta* and *N. immatura*).



Figs 1–8. *Neazonia tripleta* sp. n.: (1) Anterior portion of body; (2) Face; (3) Antenna; (4) Right fore leg; (5) Right fore tarsus; (6) Right mid leg; (7) Left hind leg; (8) Set of sensory pits of abdominal segment. Scale bars: Figs 1, 2, 7 = 1 mm; Figs 4, 6 = 0.5 mm; Figs 3, 5 = 0.1 mm; Fig. 8 = 0.05 mm.

Description: Total length of body 3.3 mm. General shape ovoid, strongly flattened, with tip of rostrum distinctly exceeding apex of abdomen.

Head: Vertex subtriangular, a bit shorter (0.36 mm) than width at base (0.41 mm), anterior margin acutely rounded, lateral margins slightly elevated, posterior margin merely excavated posteriorly at mid-length of compound eyes, disc of vertex concave, divided by longitudinal mid-dorsal ecdysial line into left and right halves. Frons about 1.9 times as long as wide, 0.79 mm long along mid-line, 0.41 mm wide, angularly rounded at apex, broadening gradually to level of antennae, then narrowing, slightly concave at level of frontoclypeal suture. Lateral carinae originating anterior to compound eye, slightly elevated, extending to level of frontoclypeal suture; submedian carinae



Figs 9–11. *Neazonia tripleta* sp. n.: (9) Abdomen and end of body in dorsal view; (10) Ventral portion of abdomen; (11) Pygofer from below. Scale bars = 1 mm.

extending slightly below the level of bases of lateral carinae, converging medially to frontoclypeal suture and parallel to lateral carinae, disc of frons elevated in upper portion, above bases of lateral carinae, elevated between submedian carinae, concave between submedian and lateral carinae; quadruplet of sensory pits in upper portion slightly below level of bases of submedian carinae; second sensory triplet pair at level of lower margin of compound eye. Clypeus 1.00 mm long; postclypeus 0.21 mm long along mid-line, 0.46 mm long along lateral line; anteclypeus 0.70 mm long along mid-line; clypellus short, 0.09 mm long. Rostrum 3-segmented, longer than body; basal segment 0.18 mm long; subapical segment, 0.26 mm; apical segment, about 1.8 mm long (tip destroyed). Antenna 0.71 mm long; scape cylindrical, slightly shorter than pedicel; pedicel elongate subglobose, with a few sensory fields; first flagellomere globular, narrower than pedicel; arista elongate.

Thorax: Thoracic nota divided by longitudinal mid-dorsal line into three pairs of plates. Pronotum distinctly wider than head including compound eyes, anteriorly produced almost to middle of compound eyes, with distinct anteromedian lobes, anterior angles slightly protruding anteriorly, lateral margins distinctly diverging posteriorly, posterior margin weakly sinuate, posterior angle with triplet of sensory pits. Pronotum along mid-line slightly shorter (0.30 mm) than vertex along mid-line, 1.26 mm wide at posterior angles. Mesonotum with wing pads wider (1.44 mm) than pronotum, distinctly longer (0.49 mm) than pronotum along mid-line, anterior margin arcuate anteriorly, lateral margins distinctly diverging posteriorly, posterior margin excavate, almost straight in median portion, lateral carinae present, elevated, delimiting disc of mesonotum, triplet of sensory pits present at posterior angle of wing pad, also single sensory pit visible on wing pad laterad of lateral carina. Metanotum with wing pads slightly wider (1.46 mm) than mesonotal wing pads, but shorter (0.36 mm) than mesonotum along mid-line, disc not delimited by carinae, wing pads extending to abdominal tergite 4, posterior margin excavate.

Prothoracic and mesothoracic coxae elongate, slender and ridged. Prothoracic femur slightly longer (0.59 mm) than prothoracic tibia (0.50 mm); prothoracic tibia subquadrangular in cross section, with rows of setae; first tarsomere 0.1 mm long with rows of plantar setae; second tarsomere 0.21 mm long, with rows of plantar setae and long apical setae; claws relatively large, 0.33 mm long; arolium wide, spatulate. Mesothoracic leg with femur shorter than prothoracic femur (0.56 mm), shorter than mesothoracic tibia (0.67 mm); mesothoracic tibia subquadrangular in cross section, slightly flattened with rows of long setae; mesothoracic tarsus 0.40 mm long; first tarsomere 0.14 mm long with rows of plantar setae; second tarsomere 0.28 mm long; tarsal claws distinct; arolium spatulate. Metathoracic femur 0.71 mm long; metathoracic tibia 1.20 mm long, round in cross section, with apical row of four teeth, covered with long setae; first tarsomere long.

Abdomen: 9-segmented, narrower than metathorax including wing pads, arcuately converging posteriorly, 1.82 mm long. Abdominal tergites IV to VIII with triplets of sensory pits on each side at posterior angles, delicately carinate at 1/3 laterad. Abdominal pleurites IV–VIII narrow with stigmal area in anterior portion. All abdominal sternites without median fissure. Pygofer (segment IX) triangular, 0.50 mm long along mid-line, 0.52 mm wide at base, with distinct narrow median incision ventrally, lateral lobes of pygofer with triplets of sensory pits near tip, posterior margins of pygofer lobes excavate, anal “combs” lobe-like.

Holotype: Nymph of IIIrd instar, specimen no. 1236 embedded in Canada balsam, Dany Azar coll. (Museum National d’Histoire Naturelle, Paris). LEBANON: Central Lebanon, Hammana/Mdeyrij outcrop; Lower Cretaceous, Uppermost Neocomian?–Lowermost Aptian (Azar *et al*. 2003).

Neazonia immatura sp. n.

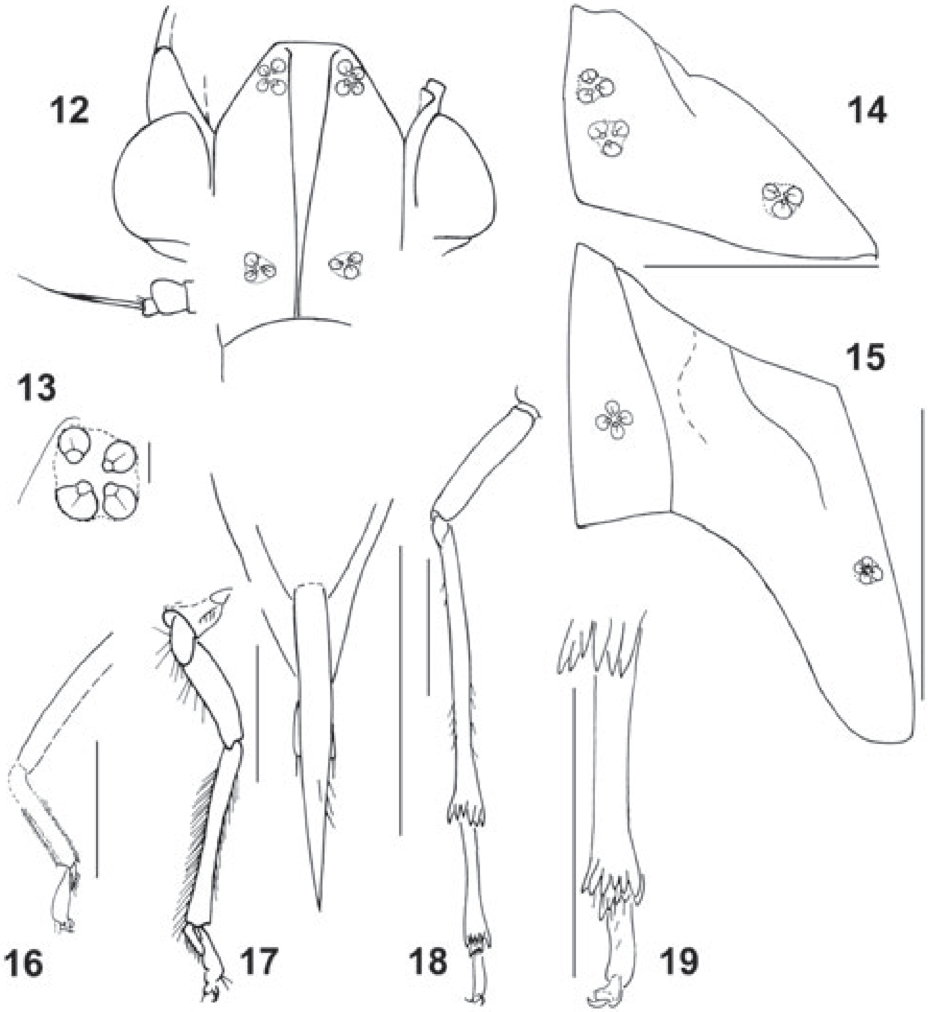
Figs 12–23, 26, 27

Etymology: Specific epithet refers to immature, nymphal stage of development of the insect preserved as inclusion in amber.

Diagnosis: More slender and elongate than *N. tripleta*, with more distinct border between thorax and abdominal segments. Anterior border of pronotum without distinct incision (distinctly incised in *N. tripleta*). Mesothoracic tibia not distinctly flattened, longer than mesothoracic femur.

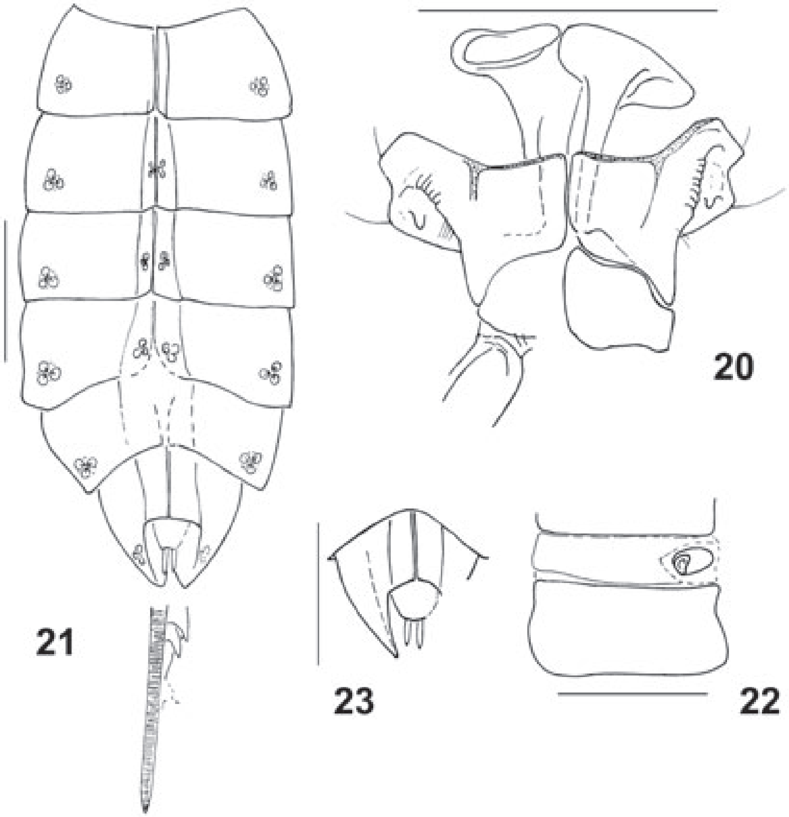
Description: Total length of body 7 mm, length with rostrum 8.5 mm. General shape ovoid, strongly flattened, with tip of rostrum extending beyond apex of abdomen.

Head: Vertex along mid-line 0.55 mm long. Frons about 1.4 times as long as wide, about 1.1 mm long along mid-line (apical portion destroyed), 0.67 mm wide, angulate



Figs 12–19. *Neazonia immatura* sp. n.: (12) Face, (13) Set of sensory pits of face, (14) Right half of prothorax, (15) Right half of mesothorax, (16) Right fore leg, (17) Left hind leg, (18) Right hind leg, (19) Right hind tarsus. Scale bars: Figs 12, 14–19 = 1 mm; Fig. 13 = 0.1 mm.

at apex, broadening gradually to level of antennae, then narrowing, slightly concave at level of frontoclypeal suture. Lateral carinae originating anterior to compound eye, slightly elevated, extending to level of frontoclypeal suture; submedian carinae extending slightly below the level of lateral carinae bases, converging medially to frontoclypeal suture and subparallel to lateral carinae, disc of frons elevated between submedian carinae, concave between submedian and lateral carinae; quadruplet of sensory pits in upper portion slightly below level of origin of submedian carinae; second sensory triplet pair at level of lower margin of compound eye. Clypeus 2.10 mm long; postclypeus 1.06 mm long along mid-line, 0.96 mm long along lateral line; anteclypeus 1.00 mm long along mid-line, clypellus short, 0.13 mm long. Rostrum 3-segmented, very long, exceeding length of body, basal segment short, subapical segment 2.37 mm, apical

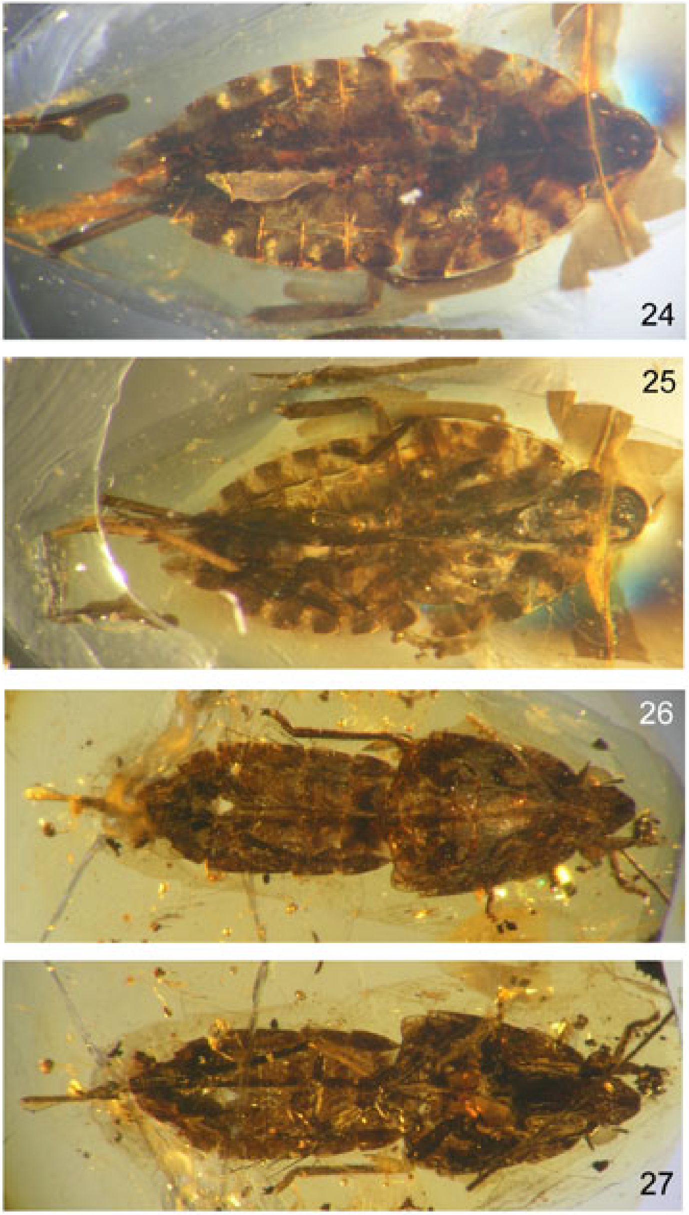


Figs 20–23. *Neazonia immatura* sp. n.: (20) Hind coxae, (21) Abdomen in dorsal view, (22) Abdominal pleural region, (23) Pygofer in dorsal view. Scale bars: Figs 20, 21, 23 = 1 mm; Fig. 22 = 0.5 mm.

segment 3.85 mm long. Antenna about 0.92 mm long, scape cylindrical, shorter than pedicel; pedicel elongately subglobose, with a few sensory fields; first flagellomere globular, distinctly narrower than pedicel; arista long.

Thorax: Thoracic nota divided by longitudinal mid-dorsal line into three pairs of plates. Pronotum 0.65 mm long along mid-line, 1.88 mm wide, median portion of disc slightly elevated, delimited by incomplete anterior carination, anterior margin protruding between compound eyes, posterior margin excavate; pair of triplets of sensory pits present laterad of median line on disc, another triplet present at posterior angle. Mesonotum with wingpads 1.00 mm long along mid-line, 2.23 mm wide, disc elevated, delimited by lateral carinae diverging posteriad, anterior margin arcuate anteriad, lateral margins diverging posteriad, posterior margin deeply excavate; quadruplet of sensory pits present on disc slightly posteriad, another quadruplet of sensory pits present near margin of wingpad, at about half of wingpad length. Metathoracic wing pads shorter (0.75 mm) along mid-line than mesonotum, 2.08 mm wide, posterior margin shallowly excavate.

Prothoracic leg with femur as long as tibia (1 mm), prothoracic tibia subquadrangular in cross section, with rows of setae, first tarsomere 0.15 mm long with rows of plantar setae, second tarsomere 0.33 mm long, with rows of plantar setae and long apical setae,



Figs 24–27. General appearance of *Neazonia*: (24) *N. tripleta* sp. n., dorsal view; (25) *N. tripleta* sp. n., ventral view; (26) *N. immatura* sp. n., dorsal view; (27) *N. immatura* sp. n., ventral view.

claws relatively big, 0.45 mm long, arolium wide, spatulate. Mesothoracic leg with femur shorter (0.88 mm) than prothoracic femur, shorter than mesothoracic tibia (1.35 mm), mesothoracic tibia slightly flattened with rows of long setae; mesothoracic tarsus 0.5 mm long, first tarsomere 0.15 mm long with rows of plantar setae, second tarsomere 0.35 mm long, tarsal claws distinct, arolium spatulate. Metathoracic coxa with small meracanthus, coxa ribbed near base anterior to meracanthus; metathoracic trochanter ring-like, about as long as wide; metathoracic femur 0.88 mm long; metathoracic tibia 2.18 mm long, round in cross section, with a few thickened setae present, with apical row of 1+2+3 teeth; first tarsomere 0.8 mm long, with 6 apical teeth, subapical setae present on teeth except for external teeth; second tarsomere short, 0.3 mm long, with 5 apical teeth, subapical setae present on teeth except for external teeth; apical tarsomere 0.33 mm long; tarsal claws and arolium distinct.

Abdomen: Abdomen 4.3 mm long along mid-line, 1.8 mm wide, 9-segmented, narrower than preceding metathoracic wing-pads. Abdominal tergites IV–VIII with triplets of sensory pits at posterior angles, and with submedian triplets of sensory pits close to the median line, delicately carinate at 1/5 of distance from lateral margin to the median line of tergite. Abdominal pleurites IV–VIII narrow, with stigmal area in anterior portion. All visible abdominal sternites without median fissure. Abdominal sternites VI and VII with pairs of subquadrangular areas (waxpads?). Pygofer (segment IX) triangular, about as long as wide (0.93 mm), with posterior margin excavate dorsad, with distinct narrow median incision on ventral margin, with triplets of sensory pits near the tip on lateral lobes, and pair of two sensory pits on ventral lobes, near apical angle. Pair of finger-like processes visible, probably dorsolateral processes of sternite IX. Anal segment triangular with median carination.

Holotype: Exuvium of Vth instar nymph, specimen No. 922AB embedded in Canada balsam, Dany Azar coll. (Museum National d'Histoire Naturelle, Paris). LEBANON: Central Lebanon, Hammana/Mdeyrij outcrop; Lower Cretaceous, Uppermost Neocomian?–Lowermost Aptian (Azar *et al*. 2003).

Neazonia imprinta sp. n.

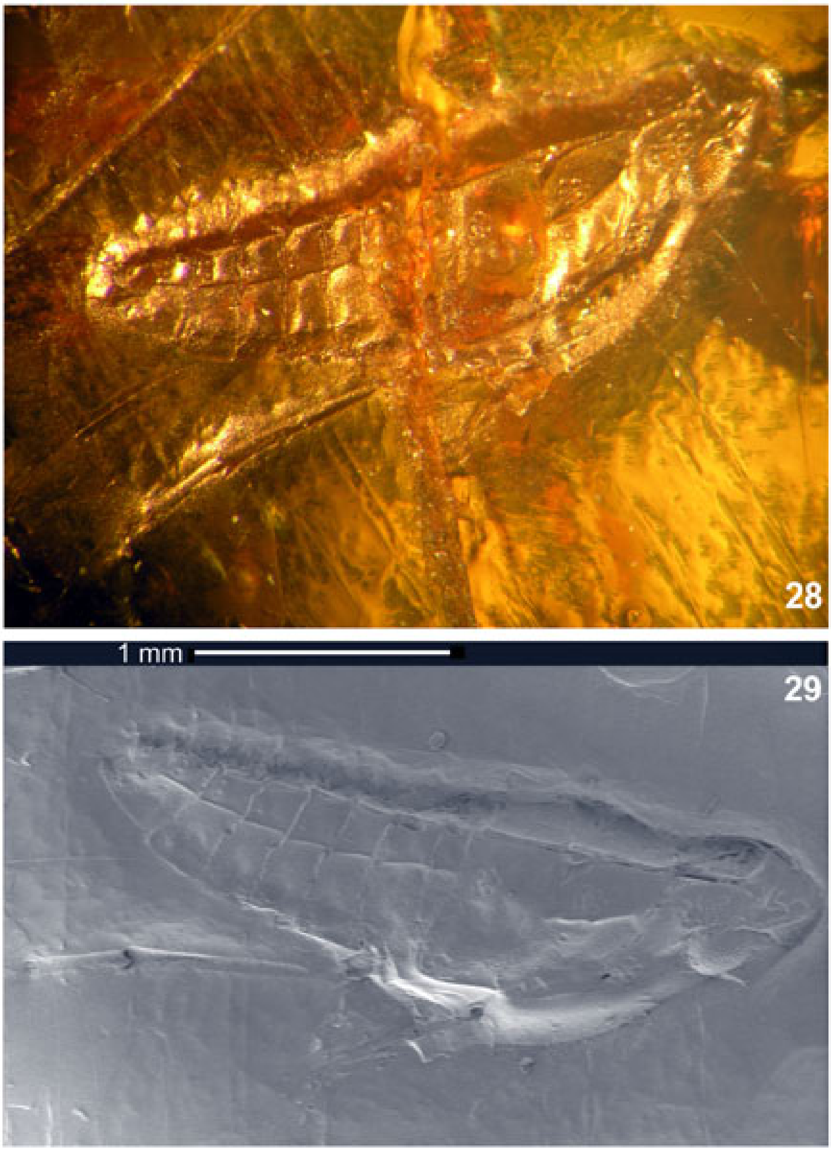
Figs 28–31

Etymology: Specific epithet refers to the state of preservation of the specimen.

Diagnosis: Less flattened than *N. tripleta* and slightly smaller. Pronotum with anterior margin not distinctly incised (incision distinct in *N. tripleta*). Quadruplet and pentaplet of sensory pits near mid-line and pentaplet of sensory pits at posterior angle of pronotum (triplet of sensory pits on posterior angle of pronotum in *N. tripleta*).
Description: Total length about 3 mm. General shape ovoid, not strongly flattened dorso-ventrally, with tip of rostrum distinctly exceeding apex of abdomen.

Head: Vertex along mid-line 0.28 mm long. Frons with quadruplet of sensory pits in upper portion. Thoracic nota divided by longitudinal mid-dorsal line into three pairs of plates. Pronotum longer (0.35 mm) than vertex along mid-line, with median portion of disc protruding anteriad; anterior angle near median line with quadruplet of sensory pits, pentaplet of sensory pits slightly posterolaterad, another pentaplet of sensory pits at posterior angle of pronotum. Mesonotum with wing pads 0.43 mm long along mid-line, about 1 mm wide, with lateral carinae delimiting disc, pentaplet of sensory pits on disc close to lateral carina. Metathoracic wing pads shorter (0.38 mm) along mid-line than mesonotum, about 1 mm wide, posterior margin shallowly excavate. Hexaplet of sensory pits on disc close to lateral carina.

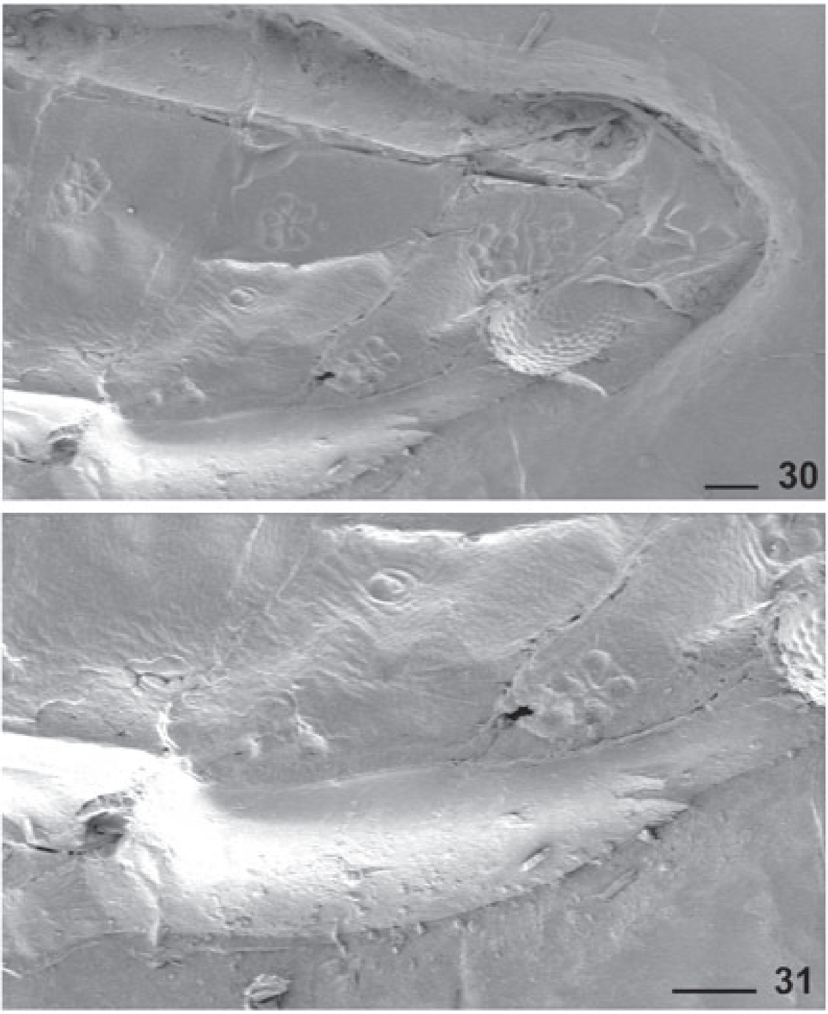
Metathoracic tibia about 1.2 mm long, with four apical teeth, probably bearing subapical setae; hind tarsus 0.6 mm long; first tarsomere 0.43 mm long with four apical teeth; second tarsomere 0.26 mm long with distinct tarsal claws and arolium.



Figs 28–29. General appearance of *Neazonia imprinta* sp. n.: (28) lateral view, light microscopy; (29) lateral view, SEM (courtesy Dany Azar).

Abdomen 1.5 mm long, abdominal tergites IV–VIII with submedian carinations at about 1/3 width laterad, with doublets of sensory pits at posterior margin mediad of carination and triplets of sensory pits at posterior angles. Pygofer apparently triangular, 0.39 mm long, with doublets of sensory pits mediad of carination at posterior margin and triplet of sensory pits at posterior angle.

Holotype: Cast of IIIrd (?) instar nymph exuvium in amber, specimen No. JG 85/7 BM 778, Aftim Acra coll. (Museum National d'Histoire Naturelle, Paris). LEBANON: Southern Lebanon, Jouar es-Souss, Jezzine outcrop; Lower Cretaceous, Valanginian–Hauterivian (Azar *et al*. 2003).



Figs 30–31. SEM of *Neazonia imprinta* sp. n. (courtesy Dany Azar): (30) anterior part of body; (31) details of thorax. Scale bars = 100 µm.

DISCUSSION

The phylogenetic relationships of the Fulgoroidea have been mainly based on characters of adults. Nymphal characters and their ontogenic development have been discussed by Emeljanov (2001), but without any proposed phylogenetic scheme. A preliminary scheme of relationships among recent Fulgoroidea based on nymphal features was proposed by Yang and Fang (1993). Nymphs of extinct Fulgoroidea have been described infrequently (Fennah 1963; Szwedo *et al*. 2004), and those that have been mentioned are limited to Eocene Baltic amber and Oligocene/Miocene Mexican amber. Recently, nymphs similar in general habitus to the species described above, but coming from Burmese amber of Albian age, have been illustrated by Grimaldi *et al*. (2002). Fulgoroidea nymphs similar to the taxa described above also occur in French amber from Archingeay of Albian age (Perrichot 2004).

The head capsules of the neazoniid nymphs described above resemble those of known achilid nymphs (Linnavuori 1951; Wilson 1983; Yang & Yeh 1994). The neazoniids differ from extant achilids by the elevated median portion of the frons, which is delimited by two carinae converging at the level of the frontoclypeal suture. Such carinae are present in an unidentified achilid nymph, described by Yang and Yeh (1994: 35–37, fig. 3A–I; Achilidae sp. 7), but these carinae diverge ventrad to the frontoclypeal suture. Submedian carinae are also present in nymphs of the genus *Cixidia* Fieber, 1866, but these carinae converge ventrally and are not fused. Submedian carinae are present in nymphs of various Derbidae (Yang & Yeh 1994), but these carinae diverge ventrally and do not converge nor are fused at the level of the frontoclypeal suture, as in the fossils described above. Submedian carinae are also present in nymphs of Delphacidae (Yang & Yeh 1994; Emeljanov 1995). These carinae are usually subparallel and do not converge nor are fused at the level of the frontoclypeal suture. If the submedian carinae are fused, as in some Delphacidae, they are unlikely to be homologous to the median carina of higher Fulgoroidea (Emeljanov 1995). These features suggest Neazoniidae should be placed close to the base of the common stock of recent Fulgoroidea, and that the fusion of the submedian carinae at the level of the frontoclypeal suture could be considered as a basal condition, and should be found in nymphs of Jurassic Fulgoridiidae.

The structure of the antenna in neazoniid nymphs seems to be very similar to that of nymphs of extant Fulgoroidea. The origin of the polymerised flagellum of Fulgoroidea is still unclear (Yang & Hsieh 1994). Emeljanov (1987) postulated that the polymerised flagellum of Fulgoroidea is a result of imaginalization of the larval antennae, while Yang & Hsieh (1994) proposed that the polymerised flagellum is derived from the filiform flagellum.

An exceptional feature of the fossil nymphs is the extremely long rostrum, which exceeds the length of the body. Such long rostra are known in adults of fossil Achilidae from Eocene Baltic amber. However, very long rostra are also known in extinct Fulgoridiidae, believed to be ancestors of the extant Fulgoroidea lineages, as well as in the poorly known genus *Knezouria* Jell from the Upper Triassic of Australia, probably representing suborder Fulgoromorpha, but with superfamilial placement not recognised. Long rostra are also known in other Mesozoic Cicadomorpha, suggesting that those insects were more often associated with woody plants, sucking sap from trunks and thick branches (Shcherbakov 2002; Shcherbakov & Popov 2002). An elongate rostrum could represent a plesiomorphic feature as it occurs in some basal fulgoroid taxa such as Neazoniidae, Cixiidae and Achilidae. On the other hand, it is also likely that a long rostrum could result from convergence, providing there is an adaptive requirement.

Sensory pits are characteristic of Fulgoroidea nymphs in all families except Tettigometridae and Hypochtonellidae (Yang & Yeh 1994). The sensory pit is a small cavity with a horizontal seta directed inwards and diverging from the cavity border, no longer than the diameter of the pit (Šulc 1928, 1929). Nymphs of extant Fulgoroidea are characterised by having two rows of sensory pits on the lateral portion of the frons (Emeljanov 2001). An ancestral condition, or general condition in Fulgoroidea as suggested by Emeljanov (2001), is that the setae of sensory pits are directed to the adjoining keel. In the nymphs of Neazoniidae, the sensory pits of the frons are arranged differently. One set of four sensory pits forms a quadruplet, with setae directed adradially, from the centre outwards in the upper portion of the frons; a triplet of sensory pits with the same configuration of setae occurs in the lower portion of the frons. According to Emeljanov (2001) the ancestral arrangement of the pits on the thorax and abdomen was probably uniform, but it became strongly and differently modified on the prothorax, pterothorax, and abdomen. Emeljanov (2001) proposed the groundplan for the distribution of sensory pits in Fulgoroidea. His proposal is that sensory pits were originally arranged in longitudinal rows, with setae directed mediad or laterad. The sensory pits on the thoracic segments in Neazoniidae are grouped in sets of three, four, five or six. The sets of sensory pits are located on the discal and lateral (pectoral) areas of the pronotum, on the discal area and at the posterior angle of the mesothoracic wingpad, and on the discal area and posterior angle of the metathoracic wingpad. The arrangement of sensory pits in groups seems to be derived with respect to conditions present in the nymphs of the extant families of Fulgoroidea. It seems probable that the position of the sensory pits in Neazoniidae is also a derived condition. In the "basal" families Cixiidae and Achilidae, the thoracic sensory pits are also rearranged with respect to the theoretical model (Emeljanov 2001). Paired sensory pits are visible only on the median part of the abdominal tergites in *N. imprinta* sp. n. Sensory pits arranged in sets are present also on the abdominal tergites, including segment IX. The shape of the sensory pits on the head, thorax and abdomen, including the pygofer, differs from that in extant nymphs. The sensory pits in Neazoniidae are pear-shaped with the base of the sensory seta narrower, whereas in extant families of Fulgoroidea pits are circular with a complete raised border, or with an incomplete raised border in the shape of a horseshoe as in Derbidae, Meenoplidae, Delphacidae and probably also Cixiidae, or divided into many segments as in Flatidae (Emeljanov 2001). Various arrangements of the sensory pits probably appeared during the diversification of Fulgoroidea in the Late Jurassic and Early Cretaceous. In order to determine which arrangement represents the plesiomorphic condition and which represent apomorphic conditions, more fossil nymphs must be examined. In *Knezouria unicus* Jell, 1993 from the Upper Triassic of Australia there are "paired areas of small tubercles" associated with a sensory hair on each abdominal segment (Jell 1993). Unfortunately no trace of such structures on the face is preserved in *Knezouria*.

The apical abdominal segment in Neazoniidae is huge, slightly longer than the preceding segment, and triangular, with the pygofer lobes extended posteriad. The median fissure between the elongated lobes of sternite IX and the presence of elongate finger-like processes, probably dorsolateral processes of sternite IX, seem to represent another important feature of Neazoniidae. Similar elongate processes in nymphs of Fulgoridae are interpreted as homologues of the gonapophysis IX (Emeljanov 1994). This suggests that in these early Fulgoroidea, the female ovipositor was not strongly reduced as in some extant families. This statement is also supported by presence of a relatively elongate ovipositor (with respect to ovipositors found in extant Achilidae) in *Niryasaburnia burmitina* (Cockerell, 1917) from Albian Burmese amber (Szwedo 2004).

Abdominal tergites VI–VIII in Neazoniidae did not bear wax-exuding areas (waxpads), which are present in extant nymphs of various families (Yang & Yeh 1994; O'Brien 1991). A pair of structures resembling waxpads is present on abdominal sternites VI and VII in *N. immatura* sp. n. Externally, these pads are similar in general structure to wax gland plates known on achilid tergites (Liang & O'Brien 2002), but the question as to whether or not these structures are really waxpads remains unanswered.

The legs of neazoniid nymphs do not differ significantly from the legs of various extant Fulgoroidea nymphs. The prothoracic tibiae are quadrangular in cross section, with rows of short setae along the margins. The mesothoracic tibiae in the fossils are also subquadrangular, with rows of setae. In *N. tripleta* sp. n., the internal row is composed of very long and dense setae. The metathoracic coxae in the fossils seem to be very similar to these structures in extant families such as Achilidae, with small meracantha, but the ribbed portion present in the fossils has not been found in extant nymphs. The metathoracic trochanters seem not to differ between the nymphs of extant families and Neazoniidae.

An interesting feature of *N. immatura* sp. n. is the presence of subapical setae on the internal teeth of the apical rows of the metathoracic first and second tarsomeres, and the fact that the second tarsomere is very short in comparison to the first tarsomere. Emeljanov (1982) proposed that the absence of subapical setae on the first and second tarsomeres of the metathoracic leg should be regarded as a plesiomorphic condition within Fulgoroidea. In contrast, Van Stalle (1986) postulated that the chaetotaxy of the metathoracic tarsomeres with a double row of a variable number of teeth and setae was a plesiomorphic condition. Later, Emeljanov (1987) stated that metathoracic first and second tarsomeres with subapical setae is a plesiomorphic feature within Fulgoroidea. This supposition is supported by the presence of subapical setae in the extinct family Lalacidae from the Lower Cretaceous (Aptian) of Brazil (Hamilton 1990). This condition is also found in families regarded as phylogenetically basal: Cixiidae (some Pentastirini), Dictyopharidae and Fulgoridae (Aluntini and Aphaenini) (Emeljanov 1971, 1979, 1982). The function of the fulgoroid tarsomere macrochaetae has not been investigated. It was postulated that the subapical setae serve to detect vibrations (Dlabola 1988), since Fulgoroidea communicate via substrate-borne vibrations (Howarth *et al.* 1990; Tishechkin 1997, 1998, 2003).

Studies on nymphs, particularly the last instar, of extant Fulgoroidea have advanced considerably in the last two decades (Emeljanov 2001). In contrast, fossil nymphs have been poorly studied. It has been assumed that until the mid-Cretaceous most fulgoroid nymphs dwelled in the soil or were cryptic on their host plants (Shcherbakov 2002; Shcherbakov & Popov 2002). Shcherbakov (2002) and Shcherbakov and Popov (2002) postulated that achilids were the first fulgoroids with mycetophagous nymphs, as are Cixiidae and Derbidae, which, with Achilidae, form a monophyletic entity based on nymphal features (Yang & Yeh 1994). Particular types of mutualistic relationships between plant roots and fungi (e.g. ectomycorrhizal, ericoid and orchid mycorrhizas) originated in the Jurassic or Cretaceous and evolved during the period of rapid angiosperm radiation in the Cretaceous (Brundrett 2002). Sorensen *et al.* (1995) suggested that early Fulgoromorpha initially evolved to feed on roots and fungal hyphae, which existed in subterranean/semisubterranean (duff) niches, much as many of their immatures do now (Wilson *et al.* 1994). All of those assumptions are supported by the nymphal morphological features of fossil Neazoniidae described above. A cryptic, flattened shape and long rostrum suggests that these nymphs could live under bark or in cavities and the presence of debris particles in a piece of amber further supports the proposed feeding association. The Neazoniidae may have lived in gymnosperm forests, which diversified during the Late Jurassic and Early Cretaceous (Taylor 1988). The Neazoniidae, Lalacidae and some undescribed fossils could be representatives of the period of intense faunistic reorganisation of insect assemblages, the "mid-Cretaceous biocoenotic crisis" (Rasnitsyn 1988; Zherikhin 1978, 1993, 2002). The mid-Cretaceous appearance and disappearance of families in the fossil record, or faunistic turnover, is clearly demonstrated by palaeoentomological data. This record may be interpreted as an endogenous community crisis evoked by competitive replacements in the early successional vegetation (Zherikhin 1993, 2002). Drastic vegetational changes in mid-Cretaceous times, during which the gymnosperm- and fern-dominated flora were replaced by angiosperm-dominated communities, was of greater importance in insect history than the Mesozoic/Cainozoic boundary with its famous dinosaur extinction.

The exact placement of Neazoniidae in a phylogeny scheme of Fulgoroidea and Fulgoromorpha remains unresolved. The results of preliminary analysis suggest that this family is near the basal lineage of extant Fulgoroidea–Cixiidae–Delphacidae and Achilidae (+Achilixiidae)–Derbidae lineages.

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